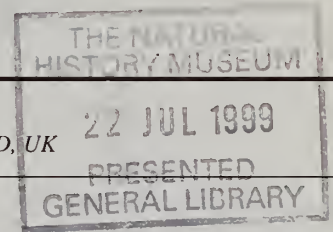


Phylogenetic relationships of Toad-headed lizards (*Phrynocephalus*, Agamidae) based on morphology

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SYNOPSIS. *Phrynocephalus* together with its sister-group, *Bufo* is most closely related to other advanced Palaearctic and African agamids. They have been regarded as the sister-group of all these species or derived from African *Agama* (Moody, 1980, morphological data) or as the sister of *Laudakia* (Joger, 1991, albumin immunology) but reassessment of morphology suggests a relationship to *Trapelus*. Parsimony analysis of 46 morphological characters, involving 54 derived states, of 25 species of *Phrynocephalus* indicates that successive branches arising from the main lineage of the genus are as follows: *P. mystaceus*; *P. maculatus*; *P. arabicus*; the *P. interscapularis* group – (((*P. clarkorum*, *P. ornatus*) ((*P. euptilopus*, *P. luteoguttatus*) (*P. interscapularis*, *P. sogdianus*))); *P. scutellatus*; *P. golubevi*; *P. reticulatus*; *P. raddei*. There is then a group of 11 species in which relationships are generally poorly resolved, although within this *P. theobaldi*, *P. roborowskii* and *P. vlangalii* are clearly closely related to each other and perhaps to *P. forsythii*, and the tuberculated species, *P. helioscopus*, *P. persicus*, *P. rossikowi* and *P. strauchi* may also form a clade. There is no clear morphological evidence that the northeastern species, *P. axillaris*, *P. versicolor*, *P. przewalskii*, and *P. guttatus* (which also extends far to the west) form a holophyletic group. *Phrynocephalus* does not appear to share its general phylogeographic pattern with other Asian reptiles and this may consequently result from dispersal rather than vicariance events. The phylogeny suggests the ancestor of *Phrynocephalus* occurred in Arabia-NW India area whence there were three independent invasions of Central Asia: by the ancestors of *P. mystaceus*, of *P. interscapularis* + *P. sogdianus*, and of *P. golubevi* and its sister group, the latter later extending north and eastwards into Mongolia, China and Tibet. *Phrynocephalus* appears to have primitively occupied aeolian sand habitats but to have spread to harder substrates from which sandy habitats were sometimes reinvaded. Degeneration of the outer and middle ear occurred in the early history of *Phrynocephalus* but was partly reversed in *P. axillaris* and the *P. theobaldi* group.

INTRODUCTION

Toad-headed agamids, *Phrynocephalus* Kaup 1825, are found in the mainly Palearctic desert regions of Asia, from Eastern Turkey and Russia to Mongolia, and southwards to southern Arabia and Pakistan. Species in the south and centre of the range of the genus are, in the main, well defined but, in the northeast, boundaries between them are often less clear and numerous nominal taxa have been described (see e.g. Zhao & Adler, 1993). This makes the total number of species in the genus uncertain but it is likely to be in excess of 30. In this paper, an estimate of phylogeny is made for 25 of the better defined species using morphological characters, including external features and some internal ones derived from the skeleton, middle ear, shoulder muscles and abdominal arteries.

RELATIONSHIPS OF PHRYNOCEPHALUS

Phrynocephalus is the sister group of the monotypic *Bufo*

Arnold 1992 which was created for *Phrynocephalus laungwalaensis* Sharma, 1978. Moody (1980) placed *Phrynocephalus* (including *P. laungwalaensis*) with what at the time was usually called *Agama* Daudin 1802, in his group 6 of the Agamidae. Within *Agama*, as then understood, this author recognised several separate genera: *Agama* s. str., *Xenagama* Boulenger 1895, *Pseudotrapelus* Fitzinger 1843, *Trapelus* Cuvier 1817 and *Stellio* Laurenti 1768. However, the name *Stellio* is unavailable (Stejneger, 1933) and the assemblage it was used to denote by Moody is paraphyletic, comprising distinct Palaearctic and mainly African assemblages (Joger, 1991; Baig & Böhme, 1997) of which the former is probably a clade and the members of the latter more closely related to such taxa as *Agama*, *Pseudotrapelus* and *Trapelus* (personal observations). Leviton, Anderson, Adler & Minton (1992) argue for the use of *Laudakia* Gray, 1845 for the Palaearctic forms, a course followed here. The more recent suggestion (Henle, 1995), that *Laudakia* should be confined to some members of this assemblage and the rest placed in *Placoderma* Blyth, 1854, requires more thorough assessment of the relationships of these lizards before it is adopted. The name *Acanthocercus* Fitzinger, 1843 is available for the remainder of the

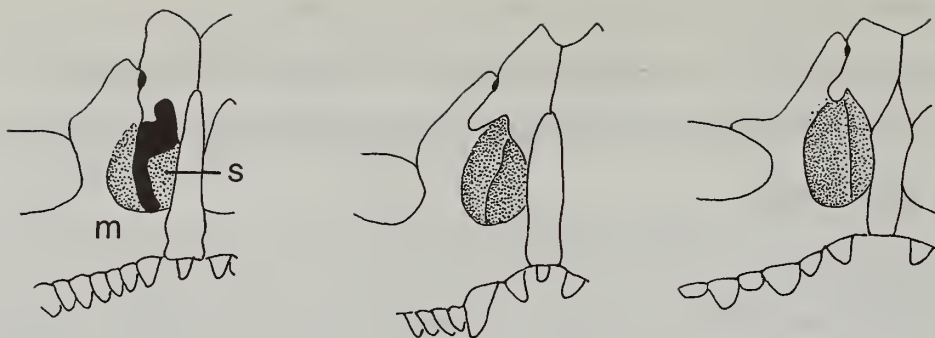


Fig. 1 Anterior views of right nasal area of skulls showing differences in contribution of the maxilla (m) to the posterior wall of the narial opening. a. Small, does not contact septomaxilla (s) (*Bufo* *laugwalaensis*). b. More extensive contribution, especially dorsally, and broad contact with septomaxilla (*Phrynocephalus mystaceus*). c. More extensive still, both dorsally and ventrally, broad contact with septomaxilla maintained (*P. euptilopus*).

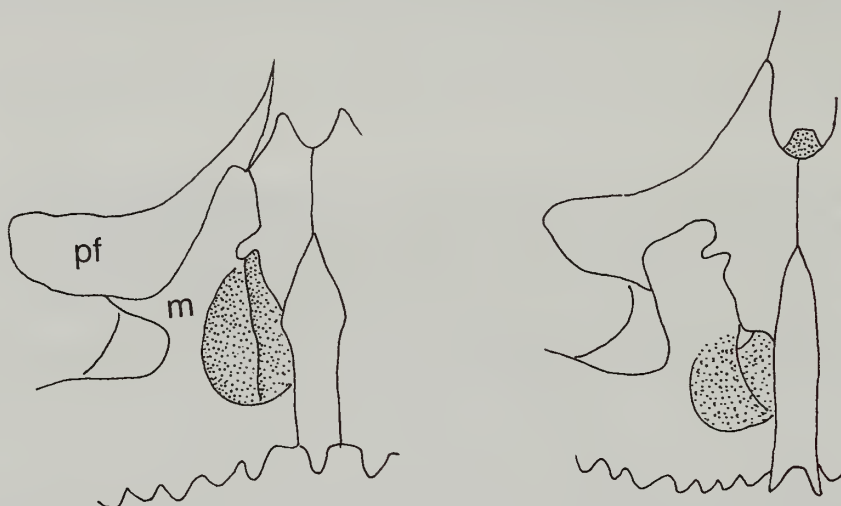


Fig. 2 Anterior views of right nasal area of skulls. a. Dorsal process of maxilla (m) tapering upwards, maxilla extending outwards below lateral process of prefrontal bone (pf) which is large (*P. euptilopus*). b. Dorsal process of maxilla blunt above, maxilla not extending markedly outwards below lateral process of premaxilla which is relatively small (*P. persicus*).

forms that Moody allocated to *Stellio* (Schätti & Gasperetti, 1994; Henle, 1995; Baig & Böhme, 1997).

Unweighted Wagner tree analysis of the morphological data presented by Moody (1980) indicated that *Phrynocephalus* was derived from a paraphyletic *Agama* s. str., while compatibility analysis, and Wagner tree analysis where characters were weighted according to their consistency index in an initial run, suggested that *Phrynocephalus* was sister to all other members of Moody's Group 6 (Moody, 1980).

Results of isozyme analysis have been interpreted as indicating that *Phrynocephalus* is the sister group of *Laudakia* (Ananjeva & Sokolova, 1990), a result in agreement with immunological studies (Joger, 1991). In contrast, a reassessment of morphology (pers. obs.) suggests that the sister group of *Phrynocephalus* + *Bufo* is *Trapelus*. Shared features that appear derived within Moody's Group 6 include the following: maxillae in contact beneath premaxilla, lateral prefrontal processes very large, palatine roof of interorbital canal narrow or absent, vomers fused, squamosal spatulate with no hook-shaped projection on its lateral margin, presacral vertebrae usually 22 or fewer; nostrils directed forwards rather than sideways, no enlarged subocular scales (reversed in some *Phrynocephalus*), external ear opening reduced in size, no spinous scales on dorsum of

neck (reversed in some *Phrynocephalus*), no caudal autotomy, scales on tail not in regular whorls; nasal passage long and flexed, depressor mandibulae muscle extends partly over tympanum.

MORPHOLOGICAL CHARACTERS USED TO ESTIMATE PHYLOGENY

Skull

1. Contribution of the maxilla to the posterior wall of the narial opening of the skull (Figure 1). Small, does not contact septomaxilla (0); more extensive especially dorsally, broad contact with septomaxilla (1); more extensive still both dorsally and ventrally, broad contact with septomaxilla maintained (2).
2. Dorsal process of maxilla (Figure 2). Tapering upwards (0); broad and ending bluntly above (1).
3. Maxilla extends clearly outwards below the anterior surface of the lateral process of the prefrontal bone (Figure 2). No (0); yes (1).
4. Relationship of maxillary and nasal bones below the lateral process of the nasal (Figure 3). Widely separated (0); more narrowly separated (1); in contact (2).

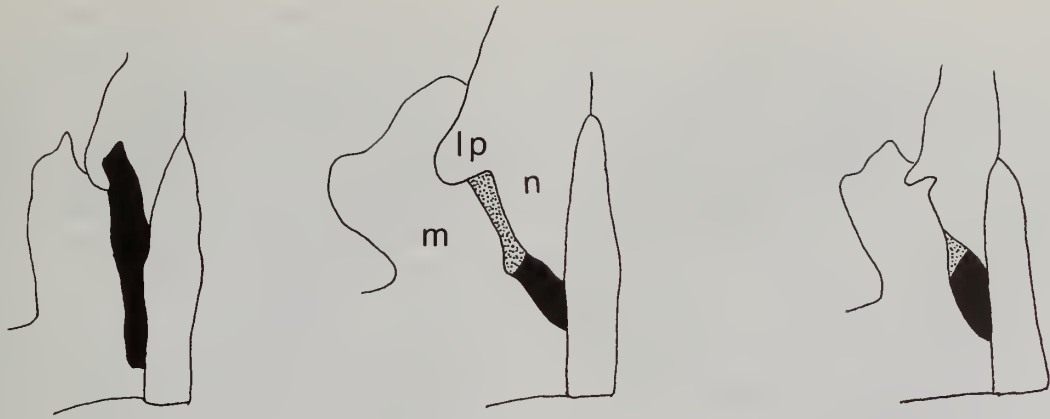


Fig. 3 Anterior views of right nasal area of skulls showing differences in arrangement of maxilla (m), septomaxilla (stippled) and nasal bones (n). a. maxilla and nasal widely separated below lateral process (lp) of nasal (*P. scutellatus*). b. Maxilla and nasal more narrowly separated below lateral process of nasal and the space filled by the septomaxilla (*P. versicolor*). c. Maxilla and nasal in contact below lateral process of nasal (*P. persicus*).

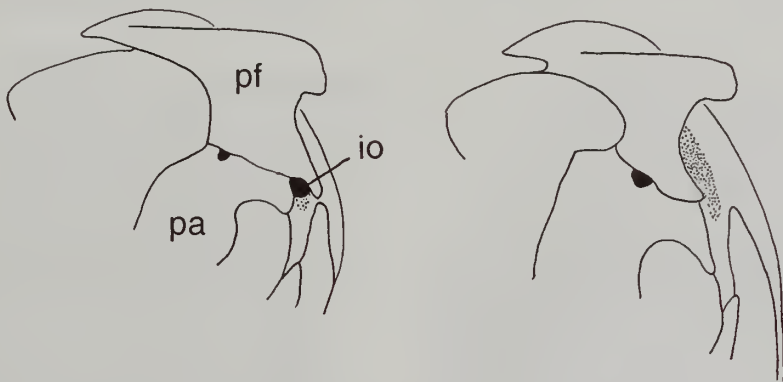


Fig. 4 View into anterior right orbit, showing width of posterior face of prefrontal bone (pf) relative to that of the posterior platine (pa) and variation in lateral extension of the prefrontal relative to the infraorbital canal (io). a. Posterior face of prefrontal broad, extends laterally across infraorbital canal. b. Posterior face of prefrontal narrow, does not extend across infrarorbital canal



Fig. 5 Difference in size of the parietal foramen (black) in adults. a. Small, diameter less than distance from the lateral edge of the parietal bone (p) (*P. scutellatus*). b. Large, diameter more than distance from lateral edge of parietal bone (*P. persicus*).

5. Maxilla in contact with septomaxilla on surface of skull below lateral process of nasal (Figure 3). No (0); yes but does not reach nasal (1); yes and reaches nasal (2).

6. Nasal bone projects laterally over maxilla anteriorly. No (0); yes (1).

7. Size of lateral process of prefrontal (Figure 2). Relatively small (0); large and extended laterally (1).

8. Width of posterior face of prefrontal bone in orbit relative to width of posterior part of palatine (Figure 4). Relatively broad
- (0); narrowed (1).

9. Prefrontal bone extends laterally across infraorbital canal (Figure 4). No (0); yes (1).

10. Size of parietal foramen in adults (Figure 5). Relatively small, its lateral diameter less than its distance from the lateral edge of the parietal bone (0); large, its lateral diameter more than its distance from the lateral edge of the parietal bone (1).

11. Body of parietal bone relative to its supratemporal processes (Figure 6). Upper surface of body of parietal bone relatively flat

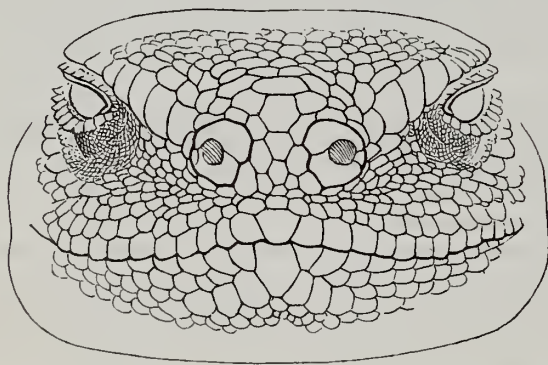


Fig. 6 Lateral profiles of supratemporal process (left) and body of parietal bone (right), arrow indicates border between the two regions. a. Upper surface of body of parietal bone running more or less smoothly into upper margin of supratemporal process (*P. mystaceus*). b. Upper surface of body of parietal abruptly raised relative to upper margin of the supratemporal process (*P. persicus*). c. Similar, but upper surface of body of parietal tuberculated (*P. scutellatus*).

and running more or less smoothly into upper margin of supratemporal processes which is relatively flat (0); upper surface of body of parietal bone abruptly raised relative to upper margin of supratemporal processes (1).

Other skeletal features

12. *Number of scleral ossicles*. Twelve (0); eleven (1); ten in some individuals (2).



Acrodonta including Agamidae usually have 12 scleral ossicles in each eye instead of the usual lizard number of 14. While *Bufo* possesses 12 there is further reduction in *Phrynocephalus*: most species and individuals have 11 ossicles but some members of at least a proportion of species in the *P. interscapularis* group have 10. This is true of *P. interscapularis*, *P. luteoguttatus*, *P. sogdianus* and *P. ornatus*. Occurrence of 10 ossicles may in fact be wider, but the other two members of the *P. interscapularis* group (*P. eutilopus* and *P. clarkorum*) are known from relatively few specimens, so checks on ossicle number have been very limited in these.

13. *Number of presacral vertebrae*. Usually 22, occasionally 23 in some species (0); usually 21, occasionally 20 (1).

Substantial data on presacral vertebral number are given by Whiteman (1978) and my own observations confirm his. Exceptions to the usual numbers occur in some species but nearly always constitute a small minority of not more than about 15% of individuals.

14. *Number of caudal vertebrae*. Usually 40–50 or more (0); usually less than 40 (1).

Again, my own observations confirm data given by Whiteman (1978).

External features

15. *Largest individuals exceed 60mm from snout to vent*. Yes (0); no (1).

16. *Outline of body viewed from above*. Robust and rounded (0); more slender (1).

17. *Position of nostrils relative to line joining anterior corners of eyes when head viewed from in front* (Figure 7). Nostrils clearly below line (0); nostrils intersecting line or above it (2); intermediate (1).

Differences in position of the nostril are associated with differences in the conformation of the distal limb of the tubular nasal vestibule. The proximal limb of the vestibule is more or less vertical in all cases, running downwards from its connection with the primary nasal chamber. Where the nostril is low, the distal limb of the vestibule is relatively short and runs obliquely upwards and outwards from the base of the proximal limb to the nostril. In animals where the nostril is high the distal limb runs more or less vertically upwards parallel to the proximal limb and is about as long as this.

18. *Number of internasal scales between the nasal scales* (Figure 7). Usually two or more – 0; usually one or nil – 1.

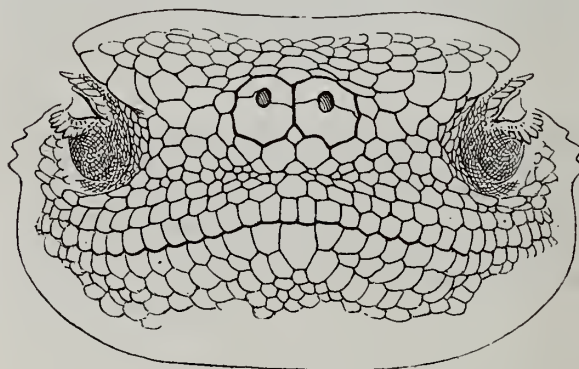


Fig. 7 Anterior views of heads showing differences in nostril position and in number of scales between nasal scales. a. Nostrils lower and separated by two or more internasal scales (*P. theobaldi*). b. Nostrils high and nasal scales in contact or separated by a single internasal scale (*P. arabicus*).

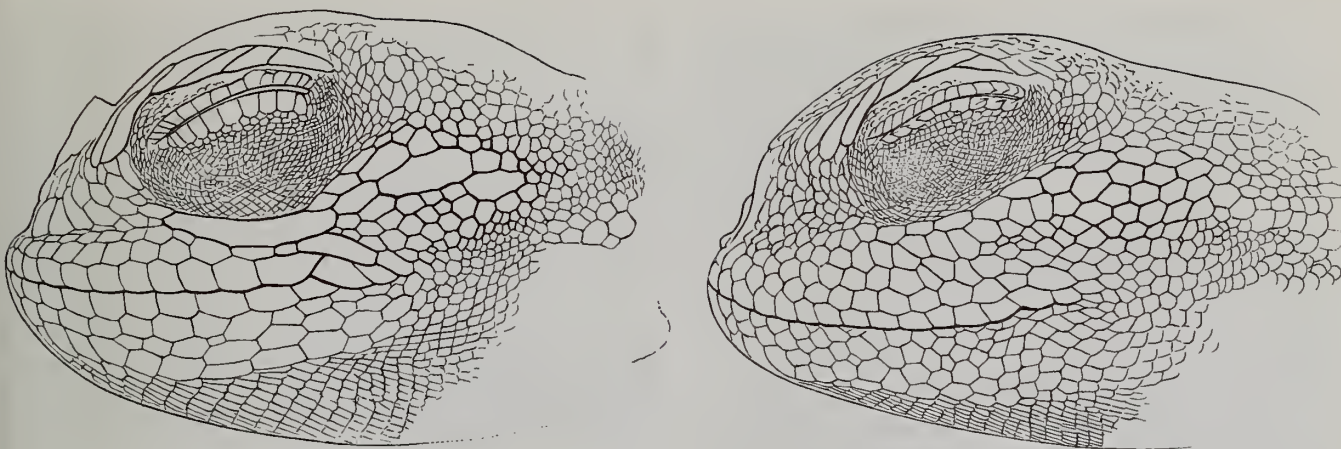


Fig. 8 Left side of head showing differences in number of horizontal rows of scales immediately above the supralabials counted below the anterior eye, and in the size of the subocular and anterior temporal scales. a. 2 or 3 rows above supralabials, subocular and one or more anterior temporals enlarged and elongate (*P. clarkorum*); b. 4–5 rows above supralabials, suboculars and anterior temporals not enlarged (*P. golubevi*).

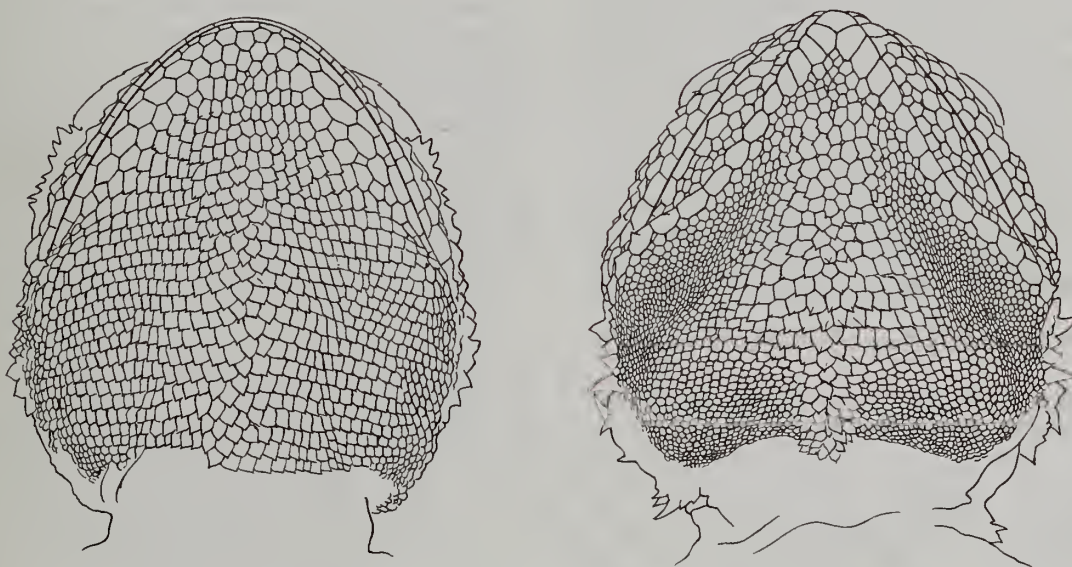


Fig. 9 Ventral views of underside of head showing differences in scalation. a. Scaling more or less uniform (*P. arabicus*). b. Scaling heterogeneous, with curved lateral row of enlarged scales, a large central patch of enlarged pointed scales, and scales at sides of throat, behind level of angle of mouth, very small and granular (*P. euptilopus*).

19. Single internasal scale with a vertical keel. No (0); yes (1).
 20. Number of horizontal rows of scales immediately above the supralabials, counted below anterior part of eye (Figure 8). Usually three rows, occasionally two (0); usually four or even five rows (1).
 21. Enlarged subocular scales (Figure 8). Not or only weakly differentiated (0); one or more enlarged, keeled, antero-posteriorly elongated scales (1).
 22. One or more enlarged, diagonally keeled and elongated scales on anterior temporal region (Figure 8). No (0); yes (0).
 23. External ear opening. Present (0); absent (1).
 24. A lateral row of enlarged throat scales beginning in mental area and curving backwards and outwards usually to the vicinity of the angle of mouth, separated from lower labial scales anteriorly by one to three rows of scales (Figure 9). No (0); yes (1).
 25. Enlarged scales in curved lateral row on throat keeled. No (0); yes (1).
 26. A large central patch of enlarged pointed scales on throat, the more postero-lateral ones directed outwards and backwards (Figure 9). No (0); yes (1).
 27. Scales at sides of throat, behind level of angle of mouth very small and granular (Figure 9). No (0); yes (1).
 28. Some scales on posterior temporal region and on sides of anterior neck enlarged, elongate and pointed, and directed outwards and upwards. No (0); yes (1).
 29. Distinct enlarged, raised, often pointed tubercles on dorsum of body. No (0); yes (1).
- Tubercles are enlarged scales that project markedly above the general level of the dorsal body skin. They may be sexually dimorphic in *Phrynocephalus*, often being more strongly

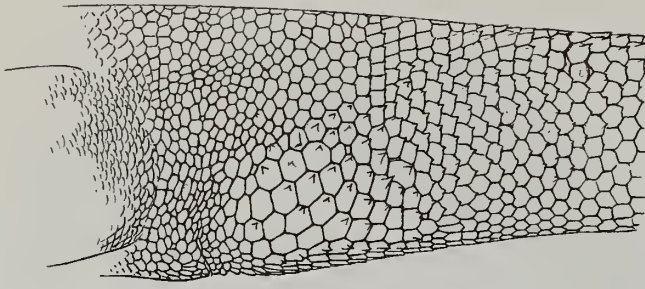


Fig. 10 Left side of tail base in *P. roborowskii*, showing enlarged spinose scales.

developed in males than females. Tubercles are frequently clumped, especially anteriorly, and there is considerable variation in the number associated in such groupings. Tubercle form is also variable and is especially narrow, pointed and elongate in *P. forsythii*, which also shows particularly strong sexual dimorphism. Although the presence of tubercles is usually a clear-cut condition, their development is sometimes sporadic and weak. For instance, many *P. theobaldi* lack them but a few animals have somewhat enlarged scales that are raised and form weak tubercles posteriorly.

30. Scales at sides of tail base distinctly enlarged and often spinose (Figure 10). No (0); yes (1)
31. Horizontal fringe of pointed upturned scales on posterior surface of proximal thigh. No (0); yes (1).
32. Subdigital lamellae on distal part of fourth toe of pes (Figure 11). With two or more keels or at least projections from the free edges of the lamellae (0); with a single keel or none (1);
33. Narrow light longitudinal stripes often present on flanks. No (0); yes (1).
34. Dark pigment frequent in mid-line area of belly in adults. No (0); yes (1).
35. Distal tail often with substantial dark pigment at least ventrally, where it may form transverse bars. No (0); yes (1).

Soft parts

36. Palatal flaps. Large (0); reduced or absent (0)
37. Tympanum. Well developed and robust (0); reduced to a delicate membrane (1); absent (2). This and other ear features of

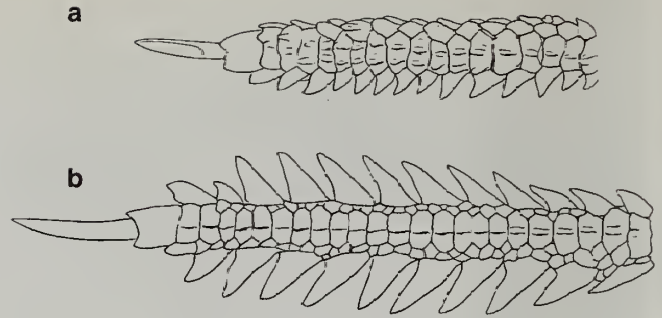


Fig. 11 Underside of fourth toes of pes (anterior edge above), showing extent of lateral fringes of pointed scales and number of keels on subdigital lamellae. a. Fringes small, especially anteriorly, two keels distally (*P. theobaldi*). b. Large fringes, single keels (*P. mystaceus*).

Bufo niceps and *Phrynocephalus* are discussed further elsewhere (Arnold, submitted).

38. Pars inferior of extracolumella. Large (0); small or absent (1)
39. Pharyngeal opening of middle ear. Large, length 15–25% of head length (0); distinctly reduced, length about 10–14% of head length (1); minute or absent (2).
40. Episterno-cleidomastoideus muscle present (Figure 12). Yes (0); very reduced (1); absent (2).
41. Episterno-cleidomastoideus muscle a single strap (Figure 12). Yes (0); with two branches (1).
42. Episterno-cleidomastoideus muscle extends anteriorly to occiput (Figure 12). No (0); yes (1).
43. Scapulodeltoideus muscle extends upwards immediately anterior to insertion of acromiotrapezius muscle on scapula. No (0); yes (1).
44. Origin of caecal artery on dorsal aorta (Figure 13). Anterior and close to mesenterica cranialis artery and well posterior to coeliac artery (0); close to and usually in front of coeliac artery, occasionally behind (1).

The caecal artery, which arises from the dorsal aorta and supplies the intestine, exhibits interspecific variation in the position of its origin on the aorta, relative to the origins of the coeliac artery, which runs to the stomach, and the mesenterica cranialis artery, which like the caecal artery supplies the intestine (Henke, 1974). In at least some *Sitana* and *Draco*, and in *Acanthocercus*,

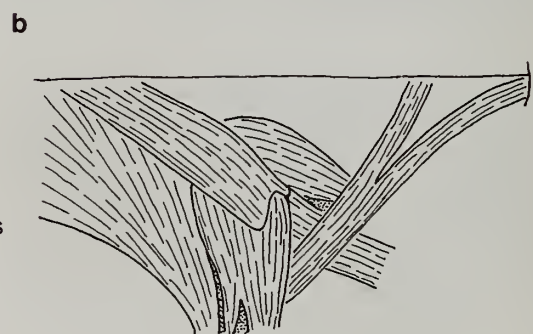
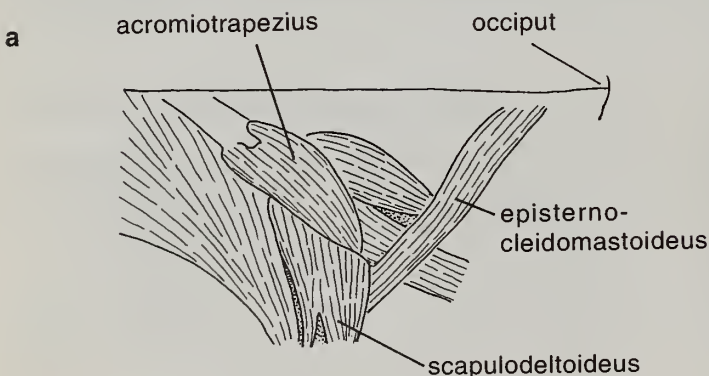


Fig. 12 Diagrammatic representations of superficial muscles of the right shoulder and neck. a. Episterno-cleidomastoideus muscle a single strap not extending to the occiput; no dorsal extension of scapulodeltoideus muscle anterior to insertion of acromiotrapezius muscle. b. Episterno-cleidomastoideus muscle divided, the anterior branch reaching the occiput; a dorsal extension of scapulodeltoideus muscle anterior to insertion of acromiotrapezius muscle present.

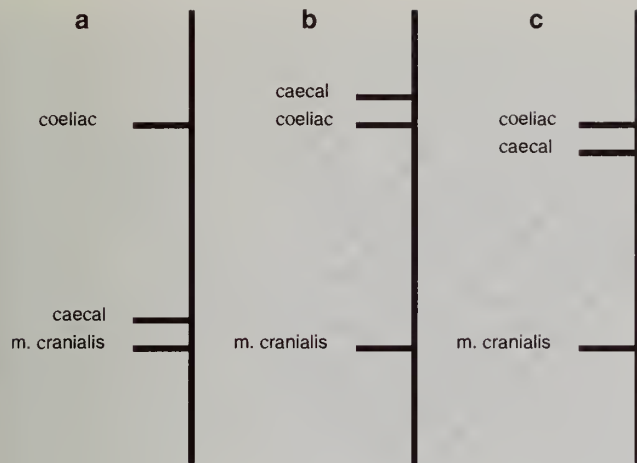


Fig. 13 Variation in position of the origin of the caecal artery on the dorsal aorta in *Phrynocephalus*. a. close to origin of mesenterica cranialis artery. b, c. Close to origin of coeliac artery.

Xenagama, *Agama* s. str., *Pseudotrapelus* and *Trapelus*, the caecal artery originates well posterior to the coeliac artery and close to and anterior to the mesenterica cranialis artery (Figure 13a). In a wide range of agamids, including *Laudakia*, the caecal and coeliac arteries originate close together, with the former usually, although not always, anterior (Figure 13b, c). (Information from Henke, 1974 and personal observations).

Within *Phrynocephalus* some species exhibit an anterior origin of the caecal artery, either a short distance in front of that of the coeliac artery or, much less commonly, just posterior to it. In contrast, the remaining members of the genus and *Bufo* species

show a posterior origin close to the mesenterica cranialis artery.

Other characters

45. *Viviparous*, giving birth to fully-formed young. No (0); yes (1).
46. *Tail used frequently in intraspecific signalling*. No (0); yes (1).

Hemipenial features

It has been suggested that features of the hemipenis delineate species groups within *Phrynocephalus* (Semenov & Danayev, 1989). These authors illustrate apparent differences in lobe length and in whether calyces are present on the lobes. However, personal observations of a wide range of species, including *P. mystaceus*, *P. maculatus*, *P. arabicus*, *P. euptilopus*, *P. interscapularis*, *P. helioscopus*, *P. theobaldi*, *P. vlangalii*, *P. guttatus*, *P. versicolor* and *P. przewalskii*, suggest that the hemipenis in these forms is consistently deeply lobed with a honeycomb structure on the outer lobe surfaces. Possibly the differences described by Semenov and Danayev result from examining hemipenes preserved in different stages of eversion.

PHYLOGENETIC ANALYSIS

The data set (Appendix 1) consists of 46 characters most of which are binary but eight include three states. *Trapelus* and *Laudakia* were used as alternative outgroups. Analysis was initially carried out using the Hennig86 program (Farris, 1988) with the options ie- and bb*, which apply branch swapping to a single tree certain to be of minimum length. When characters were ordered and *Trapelus* used as the outgroup, two trees of 110 steps were produced with a consistency index of 0.49 and a retention index of 0.79. With *Laudakia* as the outgroup two trees were again produced, with a length of 112 steps, consistency index 0.48 and retention index 0.79.

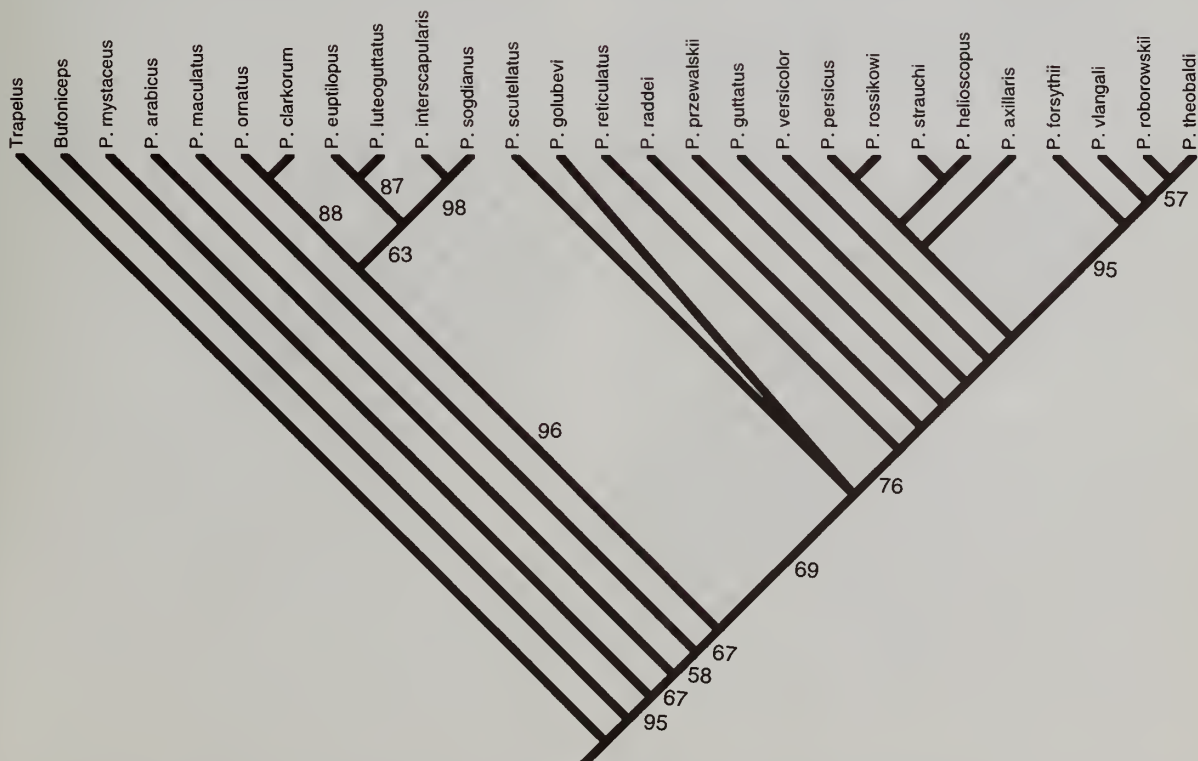


Fig. 14 Estimate of phylogeny of *Phrynocephalus* and *Bufo* using *Trapelus* as an outgroup. Tree produced by parsimony analysis using branch and bound on a tree guaranteed to be of shortest length. Figures indicate degree of bootstrap support, only that of 57% or above being shown.

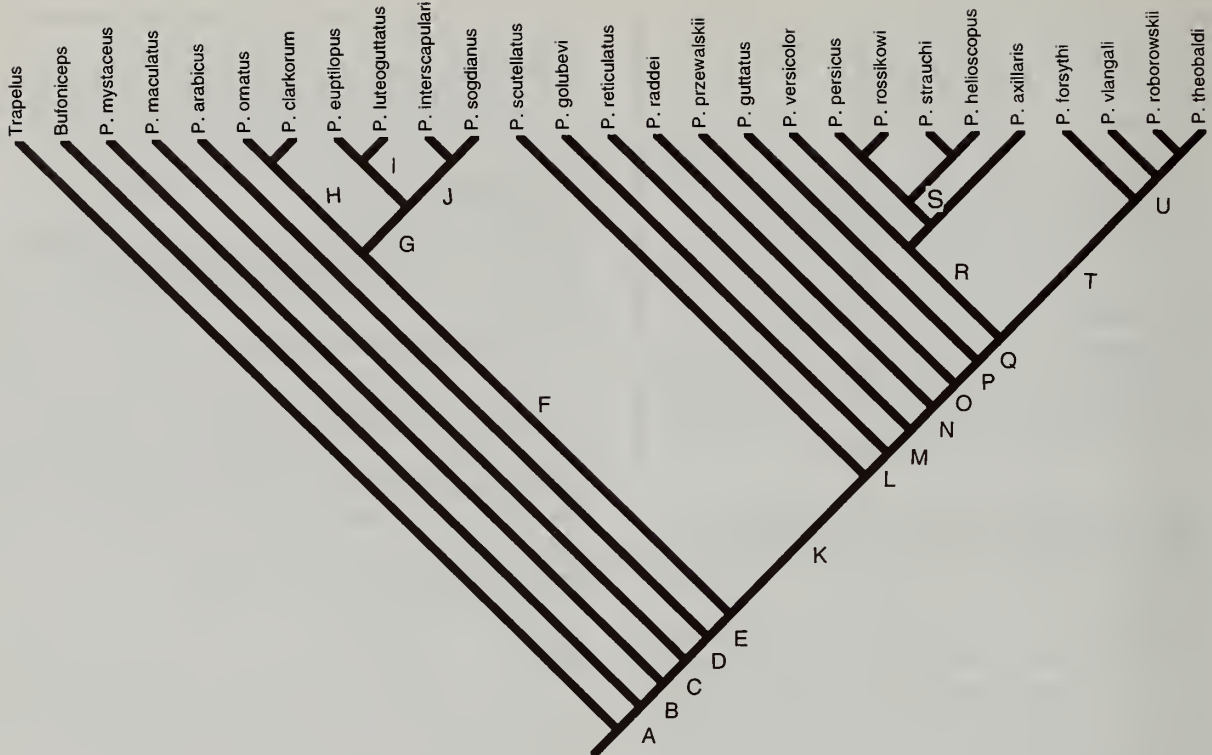


Fig. 15 Tree in Figure 14 after being subjected to successive approximations character weighting using Hennig86 program (Farris, 1988), resulting in *P. scutellatus* and *P. golubevi* being resolved as successive branches. Characters that define lettered nodes are as follows (brackets indicate some degree of parallelism; R indicates reversal). A 17, 18, (32); B 1.1, 12.1, 23, 35, 37.1, 46; C 1.2, 44; D 15; E 37.2, 38, 39.2; F 3, 12.2?, (21), 24, (36), 42; G (14), 28, 43; H 16, 22, 33; I 25, 26, 27; J (8), 19, 31; K 13, 32R; L 10, 20; M (4), 17.2R; N 17.1R; O 18R, 44R; R (29); S 29; T 30; U 6, (8), (34), 38R, (39.2R), 45.

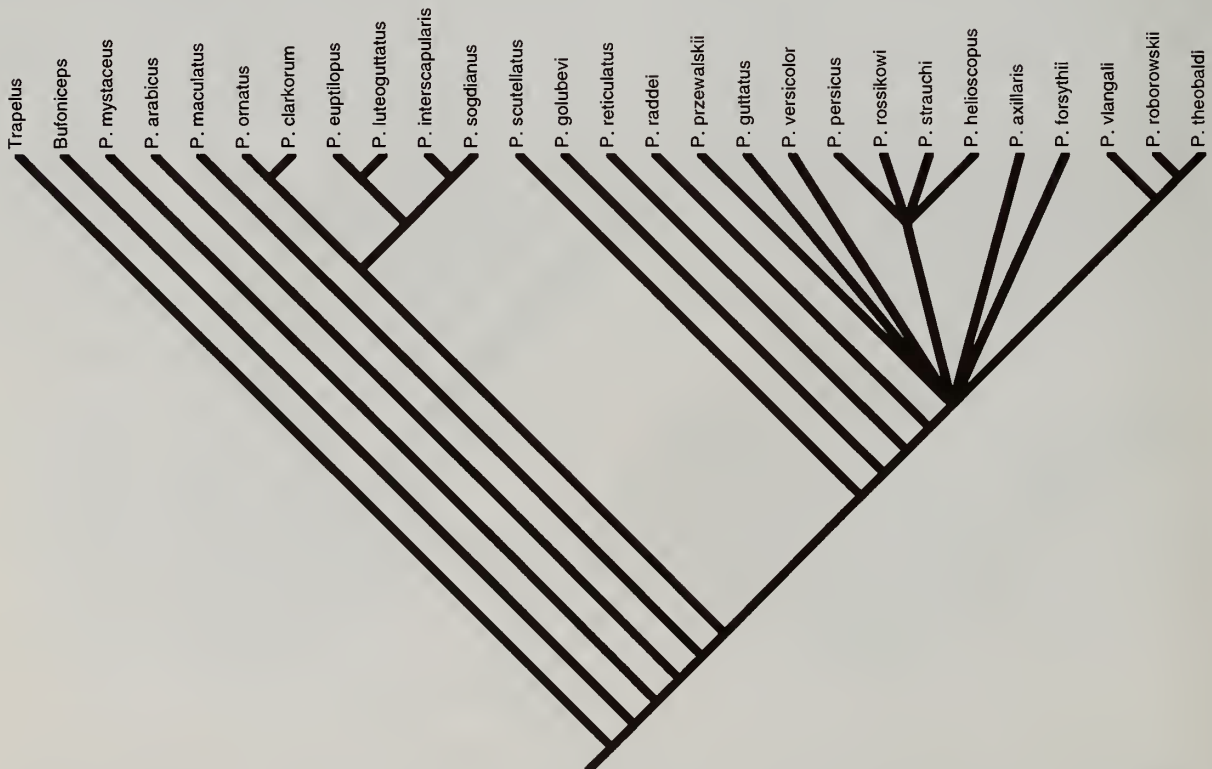


Fig. 16 Conservative estimate of phylogeny for *Phrynocephalus* and *Bufoniceps*. Only nodes supported by two or more characters of low homoplasy are shown.

In both cases the consensus has the same topology (Figure 14). When all characters were unordered, trees of 102 steps were produced which are congruent with those where characters were ordered, but with less resolution in the clade consisting of *P. przewalskii* and its nearest relatives (the topology of this region of the tree is the same as that shown in Figure 16.).

When all these analyses were repeated using the 'heuristic search' option of the PAUP 3.1.1 programme (Swafford, 1993), results were identical. Bootstrapping (100 replicates), using this programme, was also applied to the ordered tree rooted on *Trapelus* and nodes with bootstrap support over 50% are indicated in Figure 14.

Use of the successive approximations character weighting option in Hennig86 produced little change in the original tree based on unordered characters and rooted on *Trapelus*, merely resolving the trichotomy in the consensus tree involving *P. scutellatus* and *P. golubevi*, by making them successive branches on the main lineage of *Phrynocephalus*.

Principal states supporting nodes are shown in Figure 15. It will be seen that some 13 nodes are supported by two or more conservative characters that show little or no homoplasy. The other nodes are defined by single or noisy characters. A conservative tree recognising the nodes based on the former features, or with bootstrap support above 50% (and in many cases both) is shown in Figure 16.

Several nodes on the main lineage of *Phrynocephalus* are quite well supported and a number of other subclades can be recognised. Thus six species constituting a holophyletic group with marked internal structure form the *Phrynocephalus interscapularis* group consisting of *P. interscapularis*, *P. sogdianus*, *P. euptilopus*, *P. luteoguttatus*, *P. clarkorum* and *P. ornatus*. The clade has geographical coherence, occurring in western Pakistan, Afghanistan, eastern Iran and adjoining central Asia. Another well defined clade, the *P. theobaldi* group, includes *P. theobaldi*, *P. roborowskii* and the rather more different *P. vlangalii*. The similar tuberculated species, *P. helioscopus*, *P. persicus*, *P. strauchi* and *P. rossikowi* may form another unit, although it lacks marked bootstrap support.

DISCUSSION

Biogeography

Ananjeva and Tuniyev (1992) speculate about the history and biogeography of *Phrynocephalus* in the former USSR. Their complex hypothesis is difficult to assess as it is not based on an estimate of phylogeny for the species concerned and does not include other members of the *Phrynocephalus* clade.

Phrynocephalus is a characteristic element of the deserts of Palaearctic Asia, like the lacertid genus *Eremias* and the gecko assemblage including *Cyrtopodion*, *Agamura*, *Bunopus*, and *Crosso-bamon* etc. Its area cladogram is not shared with these other taxa and there is substantial sympatry between species and species groups. It therefore seems likely that parts of the genus dispersed into at least some areas of its huge range. The estimate of phylogeny suggests that the ancestor of the present species occurred in the south of the present distribution of *Phrynocephalus*, possibly within the area running from western Arabia to northwestern India. This region appears to contain the primary range of *Trapelus*, which may be the sister of the *Bufoniceps* + *Phrynocephalus* clade, and *Bufoniceps* itself occurs in northwest India. Many of the basal branches of main *Phrynocephalus* lineage are found wholly or partly in this area, including *P. maculatus* (Arabia to Pakistan), *P. arabicus* (Arabia), some members of the *P. interscapularis* group (S. Afghanistan, SW. Pakistan) and *P. scutellatus* (central and eastern Iran, S. Afghanistan and SW. Pakistan).

From this putative source area, there may have been at least a triple invasion of the presently warm and arid lowland regions of central Asia (Turkmenistan, Uzbekistan, Tadzhikistan, Kirgizstan, southern Khazakstan): by the *P. mystaceus* and *P. interscapularis-sogdianus* lineages and by the ancestor of *P. golubevi* and the members of its sister group (shown in Figure 15, 16). The latter invasion has given rise to a series of taxa in the area (including *P. golubevi*, *P. reticulatus*, *P. raddei* and the *P. helioscopus* group).

There was then apparently eastward spread: into the Tibetan region, by the ancestor of the *P. theobaldi* group and perhaps *P. forsythii*, and further north into Northwest China and southern Mongolia. On the basis of morphology, it is not clear whether extension into the latter region represents a single invasion and radiation or independent invasion by several lineages.

A variety of additional movements by particular lineages has also occurred. For instance, although within the *P. helioscopus* group *P. strauchi* and *P. rossikowi* have relatively small allopatric ranges, *P. helioscopus* is widespread in former Soviet Central Asia and the very similar *P. persicus* on the southwestern periphery of the range of this species extends into eastern Turkey and Iran. *P. guttatus* now has a broad distribution from northwest China westwards as far as the north Caspian area.

Unfortunately, there is little or no fossil record of *Phrynocephalus* and its immediate relatives. Material assigned to *Phrynocephalus* has been reported from the Pliocene of eastern Turkey (Zeroa & Chkhikvadze, 1984), but the precise relationships of these fossils are unknown and it is not even certain whether they represent a member of the clade made up of all present species of *Phrynocephalus* or if they fall outside this grouping.

This arrangement of branches on the main lineage of the *Phrynocephalus-Bufoniceps* clade correlates with species distinctness. As noted, the older southern side-branches comprise very well differentiated taxa, whereas later ones in central Asia often involve more similar species and this trend is especially marked among the relatively recent, more terminal branches in the Northwest China-Southern Mongolia region, where species are very variable, their boundaries poorly defined and their taxonomy often confused.

Structural niche

Most members of the majority of genera in Moody's Group 6 (Moody, 1980) climb to some extent. This is true of *Laudakia*, most *Acanthocercus* and *Agama* s. str., *Pseudotrapelus* and most *Trapelus*. Members of the latter genus, the likely sister-group of *Bufoniceps* + *Phrynocephalus*, spend a lot of time on the ground but many of them also climb in bushes. In contrast to these, *Bufoniceps* and *Phrynocephalus* themselves are strictly ground-dwelling, a derived condition.

There has been dispute as to whether the ancestral spatial niche of *Phrynocephalus* is soft, wind-blown sand. This is suggested by Chernov (1948), Whiteman (1978) and Semenov (1987), but Golubev (1989) and Ananjeva & Tuniyev (1992) consider the group arose in gravel and sandstone deserts. The estimate of phylogeny presented here supports the former hypothesis, with *Bufoniceps* and three of the four basal external branches of the main *Phrynocephalus* lineage being found in loose-sand habitats. (References to use of soft-sand habitats: *P. mystaceus* – Ananjeva & Tuniyev, 1992; *P. arabicus* – Arnold, 1984, Gallagher & Arnold, 1988; *P. clarkorum* and *P. ornatus* – Clark, 1992; *P. luteoguttatus* – Minton, 1966; *P. euptilopus* – Smith, 1935; *P. interscapularis* – Ananjeva & Tuniyev, 1992; *P. sogdianus* – Bannikov *et al.*, 1979). Shifts to firmer ground occurred in *P. maculatus* and independently in the ancestor of the clade containing *P. scutellatus* and its sister group. There was some

subsequent shift back to looser substrates in *P. guttatus* (Ananjeva & Tuniyev, 1992) and *P. przewalskii*.

Another indication that aeolian sand habitats are primitive is that a number of features conferring performance advantage in such environments first appear on the internal branch of the phylogeny on which these habitats are entered, that is the ancestral lineage of the *Bufo* + *Phrynocephalus* clade. These are discussed below.

Changes in morphological features

Principal changes in morphology in the history of the *Bufo* + *Phrynocephalus* clade are listed in the caption of Figure 15. A high proportion of the characters in the data set (Appendix 1) show a single change on the phylogeny. Overt reversals occur in such features as size (in *P. euptilopus*) and the pattern of arteries arising from the aorta. Simple parallelisms are quite frequent in the remaining characters, but few of these are really noisy.

Body size decreases early in the history of the main lineage of *Phrynocephalus*. Many features that appear likely to confer performance advantage in aeolian sand habitats develop at the base of the *Bufo* + *Phrynocephalus* clade and, as noted, are concurrent with entry into such habitats. These features include: lateral fringes of elongate scales on the digits that prevent the feet sinking into soft surfaces (Carothers, 1986); reduction of the keeling on the digital lamellae, which may be less necessary to reduce heat intake in soft-sand environments (Arnold, 1998); fringes of elongate scales along the edges of the eyelids, countersunk jaws, valvular nostrils, and a U-shaped nasal vestibule consisting of vertically parallel and subequal proximal and distal limbs, all of which features appear to exclude sand (Stebbins, 1943, 1944, 1948), although very long nasal passages may also protect the main nasal cavity from desiccation; skin covering the tympanum that may protect it from damage during burial activity, and lateral prefrontal processes that possibly protect the eyes during the same process.

Some of these features initially associated with aeolian sand habitats persist in less basal forms that occur on firmer substrata. Thus, toe and eyelid fringes and countersunk jaws occur in all *Phrynocephalus*, although they are less marked in species that are not found on loose sand. The outer limb of the nasal vestibule is shortened in most firm-ground forms, a shift associated with the changed position of the nostril (p. 5). This feature represents a reversion towards the primitive condition found in other Group 6 agamids. It is also associated with increased contact between the maxillary and nasal bones, either directly or via the septomaxilla. These nasal features occur in more terminal *Phrynocephalus* species on the main lineage of the genus and have developed in parallel in *P. maculatus*.

Other changes loosely associated with shift to firmer substrates include reduction in size of the lateral processes of the prefrontal bones, reduction in number of presacral vertebrae, increase in number of scale rows above the upper labial scales, increase in size of the parietal foramen of the skull and reversal in the pattern of the arteries arising from the aorta.

The high altitude *P. theobaldi* group is characterised by a number of features, including viviparity, something that often develops in cold conditions (Shine, 1985). Within this group, *P. vlangalii* develops a nostril structure that is even more reversed than in other firm-ground forms.

The external and middle ear is heavily modified in the early history of the main *Phrynocephalus* lineage, the tympanum disappearing, the extracolumella decreasing in size and the pharyngeal opening becoming very reduced or absent. These changes may be associated with greater use of subterranean rather than aerial vibra-

tion in hearing when lying under the sand. They partly reverse in the *P. theobaldi* group and perhaps independently in *P. axillaris*. Certainly the former species do not usually bury directly in the substratum and use permanent burrows instead (K. Autumn, pers. comm.)

Members of the *P. interscapularis* group possess a range of features that are rare or absent in other *Phrynocephalus* (see caption of Figure 15); their functional significance is uncertain.

Behaviour

Phrynocephalus has a number of distinctive behaviour patterns. The appearance of burial by fast lateral oscillation of the flattened body (discussed by Arnold, 1995) is concurrent with entry into aeolian sand habitats at the base of the *Bufo* + *Phrynocephalus* clade and, like some morphological features already discussed, is likely to be an adaptation to this environment. In line with this, such shimmy burial is best developed in more basal species (e.g. *Bufo* – Sharma (1978), *P. mystaceus*, *P. interscapularis* – Ananjeva & Tuniyev (1992), *P. arabicus*, *P. scutellatus*, *P. reticulatus* (pers. obs.)). Lateral oscillation often persists in species secondarily occurring on harder substrata, for instance in *P. maculatus* (pers. obs) and *P. helioscopus* (Ananjeva & Tuniyev, 1992). In such cases this behaviour may be modified and not necessarily always used for burial.

When sprayed with water, *P. helioscopus* adopts a distinctive posture in which the hindquarters are raised and the head lowered. Any liquid on the back then moves forward by capillary action in the channels between the scales (and probably by gravity when enough water is present) towards the mouth where it is ingested (Schwenk & Greene, 1987). Presumably, such behaviour permits advantage to be taken of even minor precipitation and condensation, something likely to be a significant benefit in the arid regions where *P. helioscopus* lives. *P. arabicus* from the United Arab Emirates responds to spraying very similarly (pers. obs.). As these two species are widely separated on the estimate of phylogeny for *Phrynocephalus*, this stereotyped behaviour may well be more widespread than presently known. It could not be demonstrated in *Trapelus flavimaculatus*, also from the United Arab Emirates, so it may be confined to *Phrynocephalus* and possibly *Bufo*.

Phrynocephalus species are also distinctive in using the tail for intraspecific signalling (e.g. Arnold, 1984; Ross, 1989, 1995). For instance, it may be raised, curled upwards in the sagittal plane and wagged laterally. Movements usually expose conspicuous markings on the underside of the tail, such as a dark tip and transverse bars and sometimes areas of bright pigment as well. Tail signalling has been investigated for a number of Central Asian species by Dunayev (1996), who recognises seven distinct ways in which the tail may be used (Dunayev, Figure 3). Of the species considered in the present paper, the following are listed as investigated: *P. mystaceus*, *P. maculatus*, *P. interscapularis*, *P. sogdianus*, *P. reticulatus* (as *P. ocellatus*), *P. raddei*, *P. strauchi*, *P. helioscopus*, *P. versicolor* and *P. guttatus*. When data for *P. arabicus* (Ross, 1995) is incorporated, it is apparent that more basal forms on the main *Phrynocephalus* lineage have less complex tail displays than the others. When the seven display features are treated as two-state characters (absent or present) and subjected to parsimony analysis on their own, they produce the following consensus tree which is congruent with the estimate of phylogeny based on morphology: (*P. mystaceus*, *P. maculatus* (*P. arabicus* (all other species))). However, the supposed *P. maculatus* on which Dunayev's observations were based are from the small area of Tajikistan where *P. golubevi* occurs, a species which was previously not separated from *P. maculatus*. If the animals concerned are in fact *P. golubevi*, the tree based on tail signalling is no longer congruent with that from morphology.

Ecological analogues of *Phrynocephalus*

Small diurnal lizards, that are sit-and-wait foragers, have high body temperatures when active and in many cases signal with their tails, are found in several desert systems. Apart from *Phrynocephalus*, they include the agamids *Ctenophorus* and *Tympanocryptis* in Australia, the phrynosomatid sand lizards in North America (*Uma*, *Callisaurus*, *Holbrookia* and *Cophosaurus*), tropidurines in south America (*Leiolaemus*), geckoes in southern Arabia and Somalia (*Pristurus*) and lacertids in Southwest Africa (*Meroles anchietae*). However, although they show significant parallels in morphology and behaviour, these derived features are not necessarily assembled in the same order (Arnold, 1994).

Nomenclature

As presently understood, *Phrynocephalus* is a well-defined clade defined by six synapomorphies not found in closely related agamids (numbers 1.1, 12.1, 23, 35, 37.1 and 46 in the present data set). Besides lacking these, *Bufoinceps*, the sister taxon of *Phrynocephalus*, possesses at least one apomorphy not found in the latter genus, namely a very short tail. Golubev & Dunayev (1997) suggested that *Bufoinceps* should be expanded to include *P. mystaceus*, *P. maculatus*, *P. arabicus*, *P. ornatus*, *P. clarkorum*, *P. luteoguttatus*, *P. euptilopus*, *P. interscapularis* and *P. sogdianus*. These are all basal members of *Phrynocephalus* and their inclusion in *Bufoinceps* would create a new grouping that is clearly paraphyletic and reduce *Phrynocephalus* to a smaller and less well defined clade. The suggestion should consequently be rejected.

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Appendix 1 Data set for *Phrynocephalus* and its relatives. Figures above columns refer to characters listed on pp. 2-7. - indicates no data or character uncheckable or intermediate; v indicates character variable.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Laudakia	0	0	0	0	0	0	v	v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Trapelus	0	0	0	0	0	0	0	1	0	0	0	v	v	0	v	0	0	0	0	0	0	0	0	0
3	Bufoinceps	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0
4	P. mystaceus	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2	1	0	0	0	0	1	0	0
5	P. maculatus	2	0	0	2	0	0	1	0	0	0	1	0	0	0	0	2	1	0	1	0	0	1	0	0
6	P. arabicus	2	0	0	0	0	1	0	1	0	0	1	0	0	1	0	2	1	0	0	0	0	1	0	0
7	P. ornatus	2	0	1	0	0	0	0	0	0	0	2	0	0	1	1	2	1	-	0	1	1	1	1	0
8	P. clarkorum	2	0	1	0	0	0	0	0	0	0	1	0	0	1	1	2	1	-	0	1	1	1	1	0
9	P. euphilopus	2	0	1	0	0	1	0	1	0	0	1	0	1	0	0	2	1	-	0	0	0	1	1	1
10	P. luteoguttaus	2	0	1	0	0	1	0	1	0	0	2	0	1	1	1	2	1	-	0	1	0	1	1	1
11	P. interscapularis	2	0	1	0	0	0	1	0	0	1	2	0	1	1	1	2	1	1	1	0	1	1	1	0
12	P. sogdianus	2	0	1	0	0	0	1	0	0	1	2	0	1	1	1	2	1	1	1	0	1	0	1	0
13	P. scutellatus	2	0	0	0	0	1	0	1	0	1	1	1	1	1	1	2	1	0	0	0	0	1	0	0
14	P. golubevi	2	0	0	0	0	1	0	0	1	0	1	1	1	1	1	2	1	0	1	0	0	1	0	0
15	P. reticulatus	2	0	0	1	2	0	-	0	1	-	1	1	1	1	1	1	1	0	v	0	0	1	0	0
16	P. raddei	2	1	0	2	2	0	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0
17	P. rossikowi	2	0	-	2	1	0	-	0	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
18	P. strauchi	2	1	0	1	0	0	-	0	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
19	P. persicus	2	1	0	2	2	0	0	1	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
20	P. helioscopus	2	1	0	1,2	0	0	0	-	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
21	P. forsythii	2	0	0	1	2	0	0	0	1	1	1	1	1	1	1	0	0	0	v	0	0	1	0	0
22	P. roborowskii	2	0	0	1	2	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
23	P. theobaldi	2	0	0	1	2	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0
24	P. vlangalii	2	0	1	1	2	1	0	1	-	1	1	1	1	1	1	0	0	0	v	0	0	1	0	0
25	P. axillaris	2	1	0	1	2	0	0	0	1	0	1	1	1	1	1	0	0	v	0	0	0	1	0	0
26	P. guttatus	2	0	0	1	2	0	0	-	1	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0
27	P. versicolor	2	1	0	1	2	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0
28	P. przewalskii	2	0	0	1	2	0	1	-	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0

Appendix 1 continued

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
1	Laudakia	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2	Trapelus	0	0	0	-	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
3	Bufoinceps	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
4	P. mystaceus	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	1
5	P. maculatus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1
6	P. arabicus	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1
7	P. ornatus	0	0	0	0	0	1	1	0	1	1	2	1	2	0	1	1	0	1	0	1
8	P. clarkorum	0	0	0	0	0	1	1	0	1	1	2	1	2	0	1	1	0	1	0	1
9	P. euptilopus	1	1	1	0	0	1	0	0	1	1	2	1	2	0	0	1	1	1	0	1
10	P. luteoguttatus	1	1	1	0	0	1	0	0	1	1	2	1	2	0	0	1	1	1	0	1
11	P. interscapularis	0	0	1	0	0	1	0	0	1	1	2	1	2	0	1	1	1	1	0	1
12	P. sogdianus	0	0	1	0	0	1	0	0	1	1	2	1	2	0	1	1	1	1	0	1
13	P. scutellatus	0	0	0	1	0	0	0	0	1	0	2	1	2	2	-	-	0	1	0	1
14	P. golubevi	0	0	0	0	0	0	0	0	1	0	2	1	2	2	-	-	0	1	0	1
15	P. reticulatus	0	0	0	0	0	0	0	0	1	0	2	1	2	0	0	0	0	1	0	1
16	P. raddei	0	0	0	0	0	0	0	0	1	0	2	1	2	0	0	0	0	1	0	1
17	P. rossikowi	0	0	0	1	0	0	0	0	1	0	2	1	2	2	-	-	0	0	-	1
18	P. strauchi	0	0	0	1	0	0	0	0	1	0	2	1	2	2	-	-	0	0	-	1
19	P. persicus	0	0	0	1	0	0	0	0	1	0	2	1	2	2	-	-	0	0	0	1
20	P. helioscopus	0	0	0	1	v	0	0	0	1	0	2	1	2	2	-	-	0	0	0	1
21	P. forsythii	0	0	0	1	1	0	0	0	1	1	2	0	2	0	0	0	0	0	0	1
22	P. roborowskii	0	0	0	0	1	0	0	1	1	0	2	0	1	2	-	-	0	0	1	1
23	P. theobaldi	0	0	0	v	1	0	0	1	1	0	2	0	1	2	-	-	0	0	1	1
24	P. vlangalii	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	1	1
25	P. axillaris	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	0	1
26	P. guttatus	0	0	0	0	0	0	0	0	1	-	2	1	2	0	0	0	0	0	0	1
27	P. versicolor	0	0	0	0	0	0	0	0	1	0	2	1	2	1	0	0	0	0	0	1
28	P. przewalskii	0	0	0	0	0	0	0	1	1	0	2	1	2	0	0	0	0	0	0	1